

Spatio-temporal variation in predation on artificial ground nests: a 12-year experiment

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Predation on artificial ground nests placed along four transects (alderwood, fallow, pine forest and fallow-forest edge) was studied in 1998–2009. On average, a 25.4% increase in overall predation rate was observed over the study period and increasing predation occurred at all sites. Mean multiannual predation rate differed up to 2.3-fold between transects and was highest in the alderwood and lowest in the fallow area. Despite that share of particular predators in depredation of nests was not random with respect to the studied habitats, high year-to-year variation in the pattern of predation was recorded. Between-year and between-transect changes in predation pressure were responsible for 48% of overall predation variability. Predation in one, randomly selected year was weakly related to averaged data from all 12 years, which indicates that short-term studies employing artificial nests can significantly over- or underestimate the contribution of particular species to overall predation.

Introduction

For many years, artificial nests have been used to study nest predation, and hundreds of experiments examining this phenomenon at locations all over the world have been reported (Moore & Robinson 2004). For a number of reasons, including the non-authentic appearance of the nests, experiments using artificial nests have been criticised for not revealing the true pattern of nest predation (Martin 1987, Willebrand & Marcström 1988, Wilson *et al.* 1998, Zanette 2002, Faaborg 2004, Moore & Robinson 2004, Villard & Pärt 2004). Rates of predation on artificial nests are usually significantly higher than on natural nests (Willebrand & Marcström 1988,

Wilson *et al.* 1998, King *et al.* 1999, Berry & Lill 2003, Mezquida & Marone 2003, Burke *et al.* 2004), but the opposite has also been found (Martin 1987, Davison & Bollinger 2000, Dion *et al.* 2000, Roos 2002). In addition, the predator species involved may differ between real and artificial nests (Moore & Robinson 2004, Thompson & Burhans 2004). However, the use of artificial nests also has many advantages. For example, they allow obtaining large sample sizes, creating experimental designs and exploring temporal aspects of predation (Major & Kendal 1996, Wilson *et al.* 1998, Weidinger 2001). Thus, as summarized by Faaborg (2004), artificial nest studies sometimes provide insight into predation of natural nests, but often, they do not.

In some studies, predation rates on artificial nests were found to vary between years (Wilibrand & Marcström 1988, Buler & Hamilton 2000, Mezquida & Marone 2003, Šálek *et al.* 2004), while in others, they did not (Burke *et al.* 2004). However, long-term studies using artificial nests are rare and data are usually collected for no more than 2–4 years. As a consequence, the issue of long-term variability of predation patterns has not been well explored. It should be underlined that the results of short-term studies are affected by many ecological factors (e.g. structure of predator communities, density of predator populations, availability of primary and alternative prey), which undergo high year-to-year variation. Therefore, it is expected that multiannual experiments are more helpful in estimating real and variable predation patterns.

Although artificial nests should not be used to estimate rates of real nest predation (Wilson *et al.* 1998), they may be valuable for detecting the relative importance of particular mammalian and avian predators in different habitats, and for showing true relative nest-predation risk (Pärt & Wretenberg 2002). In this study, we avoid any comparisons with real predation on ground-nesting birds inhabiting the study area and forego extrapolation from data obtained using artificial nests. Our aims were to: (i) analyze the rates of overall predation on artificial nests over a 12-year period, (ii) to describe the relative importance of particular mammalian and avian predators that rob the nests in different habitats, and (iii) to answer whether results of short-term artificial nest experiments are reliable indicators of general patterns of predation.

Material and methods

The study was conducted from 1998–2009 on the eastern bank of Lake Łuknajno (53°49'N, 21°38'E) in the central part of the Mazurian Lakeland, northeast Poland. Łuknajno is a shallow (up to 3-m deep) eutrophic lake covering an area of 6.8 km². The 10.2-km-long shoreline is poorly developed and overgrown with broad reedbeds, which are up to 100 m wide on the northern bank. The banks are low and boggy with dense willow bushes (*Salix* sp.) and belts of

alderwood (*Alnus glutinosa*). At the study site, the lake is surrounded by fallows. This area was cultivated until 1991, but since then, by the process of natural plant succession, the abandoned fields have overgrown with grasses and herbs, and more recently with shrubs, mainly pear (*Pyrus communis*), dog rose (*Rosa canina*) and common hawthorn (*Crataegus monogyna*). The fallows are adjoined to the east by a large mixed-pine forest.

Four 2-km-long experimental transects, containing 20 artificial nests each, were established parallel to the shoreline of Lake Łuknajno in four habitat types: (1) Alderwood: extending along alderwood overgrowing the lake bank, placed about 20–50 m from the lake shoreline; (2) Fallow: extending along the fallow area; (3), Edge: extending along the fallow–mixed-pine-forest edge; and (4) Pine forest: located in the mixed-pine forest. The Fallow transect was located about 200–300 m from the Alderwood transect; the Edge transect was about 100–300 m from the Fallow transect; and the Pine forest transect was about 200–500 m from the Edge transect. The transects remained unchanged over the 12-year study period.

Each year the experiment was carried out in the first half of July. One standardized type of artificial ground nest was used throughout the entire study. The nests, made of grasses and moss, were placed in the middle of 50 × 50 cm wooden boards and surrounded with 1-cm-thick and 15-cm-broad panels of deformable OASIS floral foam (produced by Smithers-Oasis Company), which recorded predators' footprints. The artificial nests were positioned on the ground in vegetation typical for a given transect, and two chicken eggs were placed in each nest. Both nests and eggs resembled to some extent natural duck nests (e.g. mallards *Anas platyrhynchos*), which were abundant in the study area (Osojca 2005). Along each transect, the nests were always spaced about 100 m apart. During the study, the nests were visited twice a day: in the early morning (4:00–6:00) and in the evening (19:00–21:00). The nests were maintained for nine days each year. They were considered depredated if at least one egg was missing or broken. Following a predation event, the depredated egg was replaced by a new one. When no footprints

were recorded on the foam, but the nest was depredated, the predator was classified as unknown. Thus, for each nest we recorded 18 nest visits per year, which resulted in 17 280 nest visits overall (2 visits per nest \times 9 days \times 20 nests \times 4 transects \times 12 years).

The potential main mammalian and avian nest-predators present in the study areas were fox (*Vulpes vulpes*), racoon dog (*Nyctereutes procyonoides*), badger (*Meles meles*), otter (*Lutra lutra*), American mink (*Neovison vison*), polecat (*Mustela putorius*), weasel (*Mustela nivalis*), pine marten (*Martes martes*), marsh harrier (*Circus aeruginosus*), raven (*Corvus corax*), hooded crow (*Corvus corone*) and jay (*Garrulus glandarius*). Because the tracks of the fox and the racoon dog are very similar, and both species are common and widespread in all the lake-side habitats, these recordings were pooled and treated as canids. Similarly, the footprints of the American mink and polecat are very hard to distinguish, but due to their different habitat preferences, these two species were treated separately. Minks inhabit the vicinity of the lake shoreline and usually do not move far from the waterbody. Live-trapping of medium-sized mustelids along the shorelines of Lake Łuknajno and three other nearby lakes (Tuchlin, Majcz Wielki and Inulec) conducted in 1995–1998, showed that the mink comprised 92% and polecat 8% of all trapped animals (M. Brzeziński unpubl. data). Thus, all mink/polecat footprints recorded at the artificial nests placed along the transect adjoining the lake shoreline (Alderwood) were treated as mink tracks, although the presence of the polecat in this habitat could not be totally excluded. On the other hand, footprints recorded along transects more distant from the lake were recognized as polecat tracks because the probability of mink movements far from the lake shoreline was very low (based on radio-telemetry data; M. Brzeziński unpubl. data). The conclusion that minks move almost exclusively along the banks of waterbodies is supported by findings of previous studies on mink activity (Gerell 1970, Harrington & Macdonald 2008, Melero *et al.* 2008). Additional analysis, not presented in this study, indicated that excluding the mink and polecat had no significant effect on the redundancy analysis performed (*see below*). Corvids were treated

as one group; however, footprints of the jay were recorded only in the pine-forest and forest-edge habitats, while those of the hooded crow were recorded exclusively along the lake shoreline and in open areas. Ravens, although recorded in the study area, were extremely rare visitors to the artificial nests.

To avoid possible problems of spatial autocorrelation of the results from adjacent nests and pseudoreplication, the results from all visits of all nests were pooled and predator pressure was expressed as a percentage of depredated nests among all nests exposed during the 9-day period (for each transect and year independently). The error structure of this continuous variable (predator pressure) was normal (Kolmogorov-Smirnov test: $p > 0.592$ in all cases). Variability in predation pressure was examined using General Linear Models (GLM) with the percentage of depredated nests among all nests as the dependent variable, while habitat type was used as a fixed categorical factor, and year as a covariate.

The importance of each predator species in overall predator pressure was also tested. The share of nests depredated by each predator in a given habitat and year was evaluated. In order to assess the similarity of predation pattern of a particular predator and to link the predator with habitat type, Redundancy Analysis (RDA) was implemented using the CANOCO software (Lepš & Šmilauer 2003). The contribution of each predator to overall predation was used as species data (i.e. dependent variables), with habitat type as environmental data (i.e. explanatory variables). To exclude possible trends, year was added as a covariable. The “other carnivores” category was excluded to restrict the analysis to identified predators. The Monte Carlo test with 500 permutations was used to test the significance of the canonical axes (Lepš & Šmilauer 2003).

Further analysis of the data was performed to identify the likely factors (year and habitat) influencing the contribution of a particular predator to overall depredation. Since the share of nests depredated by each predator in a given habitat and year add up to 100%, they were mutually negatively correlated. Therefore, Principal Components Analysis (PCA) with orthogonal varimax rotation for data reduction and the exclusion of collinearity was applied. Three

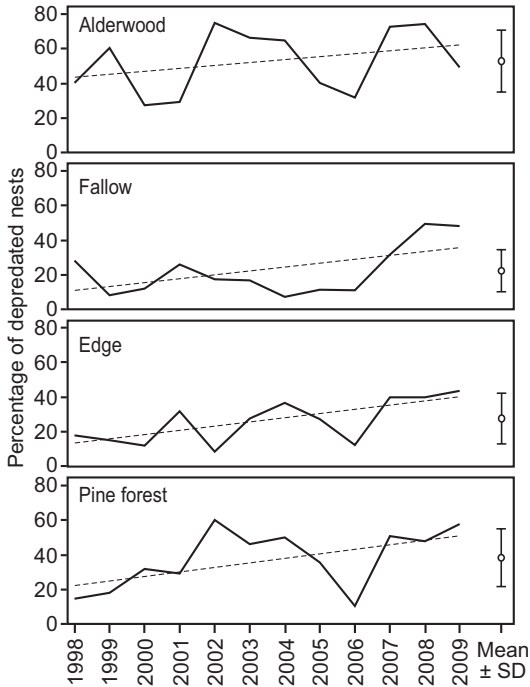


Fig. 1. Variability of predation on artificial nests during 12 years in four habitat types in the Mazurian Lakeland (NE Poland). Solid lines indicate year-to-year variation in predation pressure and dashed lines indicate trends. Arithmetic mean \pm 1 SD is also shown.

components with eigenvalues greater than one were extracted and used for further analysis. The components were normally distributed (Kolmogorov-Smirnov test: $p > 0.152$ in all cases) and were used as dependent variables in GLMs, with habitat type and year as a fixed factor and covariate, respectively. Variance homogeneity was checked each time with Levene's test. In one case, where the assumption of variance homogeneity across the groups was not met, Welch's test with adjusted degrees of freedom was additionally used to protect against inflating Type I error (Quinn & Keough 2002).

For the GLMs explaining overall predation as well as the contribution of each predator species to this predation, the most parsimonious models were selected on the basis of the Akaike Information Criterion corrected for small samples (AIC_c) (Johnson & Omland 2004). Finally, an attempt was made to compare one-year results with results obtained during 12 years. For each transect, the share of a particular predator

species in all depredations for a given year was correlated (Spearman's rank correlation) against the average share of this species over 12 years. As a result, an average correlation between one and 12 years was obtained for each habitat. SPSS 15.0 software was used for the statistical analyses.

Results

Overall variability in predation

Overall predation varied between transects and years, with the full model being most parsimonious according to AIC_c ($AIC_c = 8414.466$) as compared with models containing year only ($\Delta AIC_c = 6595.443$) or habitat only ($\Delta AIC_c = 2556.694$). Predation rates increased significantly during the 12-year study and this pattern was observed for all transects. The mean annual increase in overall predation rate, assessed by the linear model, was 2.1%, which resulted in a 25.4% increase over the entire study period (GLM: $F = 11.38$, $p < 0.0001$). Predation patterns in the four habitat types were not cyclic (Autocorrelation analysis, results not shown). Predation rates showed significant differences between habitat types (GLM: $F = 13.24$, $p < 0.0007$, Fig. 1). Mean multiannual predation rate for the Alderwood transect was 52.3% (18.17 SD) and varied from 26.9% in 2000 to 75.0% in 2002 (Fig. 1). Mean multiannual predation rate was lowest for the Fallow transect (22.3%; 14.76 SD), and varied more than 7-fold between years (7.0%–49.4%). Predation pressures in the Edge (mean multiannual predation rate 26.0%; 12.36 SD, range 8.0%–43.3%) and Pine-forest (mean multiannual predation rate 37.6%; 16.96 SD, range 10.0%–60.0%) transects were intermediate. Between-year and between-habitat changes in predation pressure accounted for 48.0% of the variability in overall predation. The assumption of variance homogeneity across all groups was met (Levene's test: $F = 2.51$; $p = 0.071$).

Predation pattern

The nest-robbing activities of predators were

significantly related to habitat type as revealed by Redundancy Analysis (RDA) (Monte Carlo permutation test: first canonical axis, F -ratio = 17.76, p = 0.002; all canonical axes, F -ratio = 12.98, p = 0.002). During the whole study the mink represented 35.5% and canids 32.0% of all predators identified along the Alderwood transect (Fig. 2) and until 2004, they were the main predators taking eggs from the artificial nests at this site. However, year-to-year variation in the depredation activity of the mink and canids was high. For example, canids were responsible for 95% of nest losses in 1999, but in the following year they did not take any eggs and the dominant predator was the mink, which caused 86.7% of depredations. Along the Fallow transect, marsh harriers were identified as nest predators in every year and, on average, were the most active predators throughout the study. They comprised nearly 60% of identified nest predators in the Fallow habitat and were responsible for about 90% of total nest losses in some years (Fig. 2). Artificial nests placed along the Edge transect were depredated by a variety of predators. The polecat was the predominant predator and was responsible for 39.0% of the identified depredations (Fig. 2). Nest depredation along the Pine-forest transect was dominated by the polecat to an even greater extent: this predator was responsible for nearly 60% of all identified cases of nest robbing. The polecat was recorded as a nest predator throughout the entire study period in the Pine forest and Edge transects (Fig. 2). In these habitats, nests were also depredated by canids, pine martens, marsh harriers and corvids with high year-to-year variability, although high activity of these predators was recorded in only a few years of the study (Fig. 2). Badgers appeared to show low levels of habitat specialization (*see* Fig. 3). They started to take eggs in 2004 and since then remained an important nest predator in all habitats (Fig. 2).

The predation pattern was highly similar along the Edge and Pine forest transects, as revealed by the RDA (Fig. 3), but was very different from that observed in the two other habitats. However, partial correlation (controlled for year effect to exclude trends) of overall predation between the habitats over the 12 years was significant only for the Alderwood–Pine forest pair (r = 0.62, df = 9, p = 0.043).



Fig. 2. Contribution of particular predator species (or species group) to overall predation on artificial nests in four habitat types during 1998–2009 in the Mazurian Lakeland (NE Poland). Undetermined predators are excluded.

Principal Components Analysis extracted three orthogonal (i.e. uncorrelated) components with eigenvalues greater than one, which account for over 63% of variability in the composition of predators depredating artificial nests (Table 1). The first component explains differences in the contribution of canids and minks on the one hand, and corvids and polecats on the other (negative values of the component indicate the importance of corvids and polecats, whereas positive values indicate the importance of canids and minks). The second component characterizes the importance of the pine marten (positive) and badger (negative), whereas the third compo-

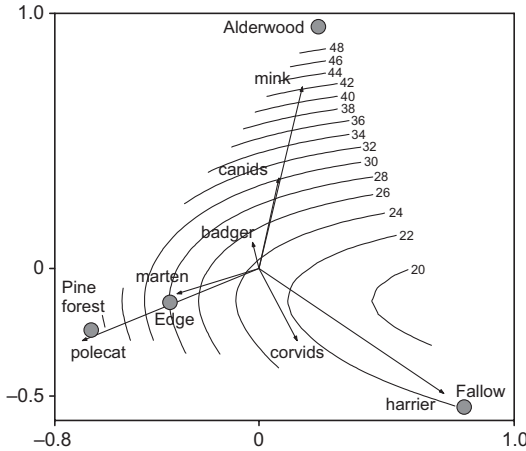


Fig. 3. Predator species–habitat type Redundancy Analysis (RDA) biplot showing variability of predation pressure by different species on artificial nests in the four habitats. Centroids of the four habitat types are indicated by grey dots. Variability of predation pressure, expressed as the percentage of nests depredated, is shown with isolines using the General Additive Model for visualization.

nent explains the importance of the marsh harrier (positive) and polecat (negative) (Table 1).

The first component showed significant variability between habitats (GLM: $F = 19.08, p < 0.0001$), but did not change during the study period (GLM: $F = 3.24, p = 0.079$). Alderwood was characterized by high values of component 1, indicating the importance of canids and the

Table 1. Pearson correlation coefficients of the three components extracted by Principal Components Analysis (PCA) with orthogonal varimax rotation, with the original contribution of each predator to overall predation on artificial nests. Only correlations at $p < 0.001$ are shown.

	Components extracted		
	1	2	3
Canids	0.728		
American mink	0.713		
Badger		-0.879	
Pine marten		0.606	
Polecat	-0.477		-0.724
Marsh harrier			0.864
Corvids	-0.471		
Eigenvalues	1.57	1.47	1.42
% variance explained	22.5	21.0	20.2

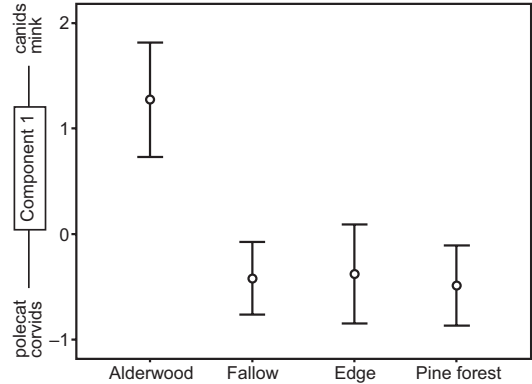


Fig. 4. Mean (\pm 95% CI) values of the first PCA component (see Table 1), interpreted as the relative importance of predation by canids and mink vs. polecat and corvids in the four habitat types.

American mink, whereas that of corvids and polecat was low in this habitat type (Fig. 4). Between-habitat variability accounted for 55.0% of the overall variability of component 1. The model with habitat used as a fixed factor was most parsimonious ($AIC_c = 118.149, \Delta AIC_c = 0$) as compared with the full model ($\Delta AIC_c = 1.027$) and model containing year only ($\Delta AIC_c = 19.864$). The assumption of variance homogeneity across habitats was met (Levene’s test: $F = 0.53, p = 0.665$).

The contribution of the pine marten and badger to overall predation on the artificial nests showed variability between habitats (GLM: $F = 3.38, p = 0.027$): the importance of the marten was highest for the Pine forest and lowest for the Alderwood, while the opposite pattern was observed for the badger (Fig. 5). However, the full model was less parsimonious ($\Delta AIC_c = 4.276$) as compared with the model containing year only ($AIC_c = 107.610, \Delta AIC_c = 0$), while the model containing habitat only was least informative ($\Delta AIC_c = 33.652$). The relative contributions of the pine marten and badger to nest depredation showed a highly significant trend over 1998–2009 (GLM: $F = 111.99, p < 0.0001$). During the study period, the importance of the pine marten decreased, while that of the badger increased (Fig. 5).

The third component showed distinct variability among the habitats (GLM: $F = 55.49, p < 0.0001$) and these differences were stable

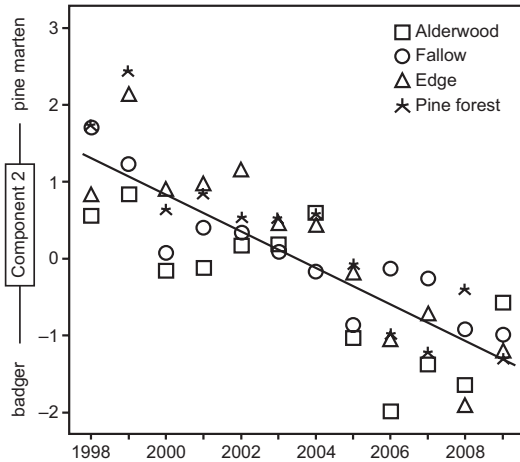


Fig. 5. Variability of the second PCA component (see Table 1), interpreted as the change in relative importance of predation by the pine marten and badger in the four habitat types.

during the study period (GLM: $F = 2.35$, $p = 0.132$). Along the Fallow transect, the highest predation was by the marsh harrier and lowest by the polecat, while the reverse situation was observed along the Pine forest transect (Fig. 6). Habitat type accounted for 77.1% of the variability of component 3 and this model was the most parsimonious ($AIC_c = 107.211$, $\Delta AIC_c = 0$) as compared with the full model ($\Delta AIC_c = 1.976$) and the model containing year only ($\Delta AIC_c = 31.751$). The assumption of variance homogeneity across the groups was not met but Welch's test adjusted for variance heterogeneity was highly significant (asymptotically F -distributed statistic = 41.92, $df_1 = 3$, $df_2 = 21.85$, $p < 0.0001$).

In general, the contributions of particular predator species to predation recorded in each year were positively correlated with their contributions for the whole study period (years 1998–2009 pooled). However, these correlations were weak and 25 out of 48 were insignificant (Fig. 7).

Discussion

Deficiencies of the artificial nest method

Artificial nests differ from natural nests in a number of important respects that may influence

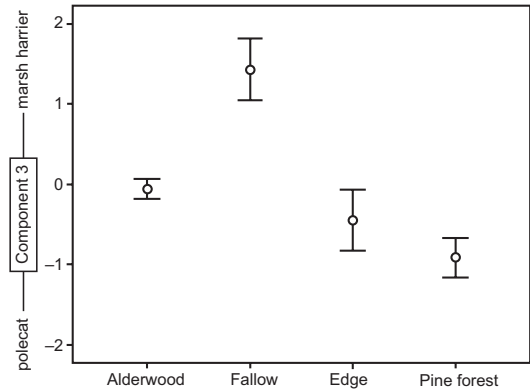


Fig. 6. Variability (Mean \pm 95% CI) of the third PCA component (see Table 1), interpreted as the relative importance of predation by the marsh harrier and polecat in the four habitat types.

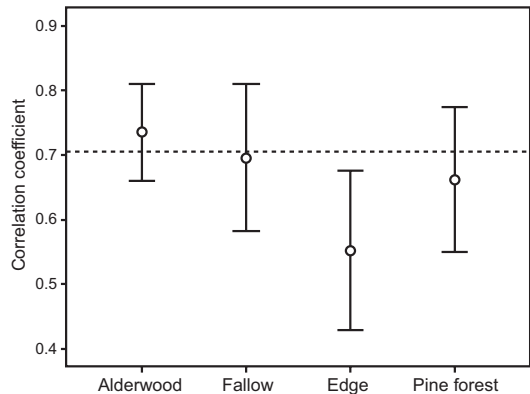


Fig. 7. Mean (\pm 95% CI) values of Spearman's rank correlation coefficients between the share of a particular predator species in all depredations during one year and the share averaged for 12 years for each habitat independently. The horizontal line indicates the threshold of significance ($\alpha = 0.05$) of the coefficients.

predation rates. Despite some reports of a correlation between the depredation of natural and artificial nests (Buler & Hamilton 2000, Ackerman *et al.* 2004), the latter are easier to find and thus predation rates are usually much higher than in the former (Willebrand & Marcström 1988, Wilson *et al.* 1998, King *et al.* 1999, Mezquida & Marone 2003, Burke *et al.* 2004). Moreover, artificial nest predation rates have been shown to vary with egg type, nest appearance, nest density and placement, degree of nest concealment and time of exposure (Major & Kendal 1996, Lindell 2000, Berry & Lill 2003, Opermanis 2004). The use of

different methodologies creates different biases, making the comparison of studies problematic (Whelan *et al.* 1994). It is obvious that a uniform methodology is essential in order to compare results between and within studies (Thorington & Bowman 2003). However, the depredation of artificial nests can be used as an index of the probability of different predator species robbing real nests in different habitats and landscapes, or as a relative index of spatial and temporal variation in nest predation risk (Roos 2002).

For the aforementioned reasons, we avoided comparisons with other studies and instead concentrated on comparing the results from consecutive years and between habitats provided by the multiannual methodological regime of the present study.

Spatial variation in predation rates and predator activity

In general, the nature of the habitat determines the density and activity of carnivores and raptors, and thus, predation rates may differ significantly according to habitat type (Martin 1987). Comparisons of the overall levels of predation along different transects showed that some habitats are more attractive to predators than others. However, generalizations of our results should be avoided since habitat type was not replicated. Differences between transects may simply be related to habitat types in the study area, but may also result from other characteristics, such as distance to the lakeshore, human activity and landscape connectivity. On the other hand, predators that predominate in a certain habitat may be more efficient egg robbers than those from other habitat types. For example, predation in the Fallow transect was shaped by the activity of marsh harriers, which were the main nest predators, but they were not as effective as the carnivores that depredated most nests in other habitats. Badgers were highly active in all habitats despite several previous reports showing their preference for rather open areas as feeding grounds (Seiler *et al.* 1995, Holmala & Kauhala 2009). The high efficiency of badgers in robbing artificial ground nests is likely to be connected with their long-distance movements within ter-

ritories (Kowalczyk *et al.* 2006), rather than their inclination to search for nests. Hounscome and Delahay (2005) reviewed the feeding behaviour of badgers in Europe and found that birds form a rather small part of their diet. However, due to their opportunistic feeding habits, badgers may locally exploit ephemerally abundant food resources such as broods of ground-nesting birds (Erlinge *et al.* 1984). Besides badgers, the only other predators found to rob eggs in all types of habitats were canids, but the multiannual variation in their activity in particular habitats was high. Their nest depredation activity remained relatively high in Alderwood overgrowing the lake bank, probably due to the contribution of racoon dogs, which are reported to prefer habitats adjoining waterbodies and deciduous forests (Kauhala 1996, Holmala & Kauhala 2009). However, other studies have failed to show distinct habitat preferences of racoon dogs (Drygala *et al.* 2008) and foxes (Cavallini & Lovari 1994, Holmala & Kauhala 2009) in a mosaic landscape, and it is probable that both canid species temporarily choose habitats with the highest food abundance (Cavallini & Lovari 1991). In the community of predators, two mustelids — the American mink and polecat — played a significant role in depredating artificial nests in the Alderwood, Edge and Pine-forest transects, although their predation activity in particular transects was estimated indirectly, based on habitat preferences of these two species (*see* methods for details). Irrespectively of this methodological assumption, the importance of the mink and polecat as nest predators was reduced following an increase in the badger population (*see* below). Corvids were responsible for a low number of nest depredations and this result is at odds with the findings of numerous artificial nest studies (Angelstam 1986, Andrén 1992, Buler & Hamilton 2000, Roos 2002). In agricultural landscapes, high nest losses are usually related to the high density/activity of corvids; however, different species depredate nests more or less intensively according to the proportion of forest in the area (Andrén 1992, Andrén *et al.* 1985, Huhta *et al.* 1996). On the other hand, some studies found that ground nests were significantly more often depredated by mammals than by corvids (Söderström *et al.* 1998, Šálek *et al.* 2004).

Predators shared “egg resources” in all habitats, but the predation pattern was highly dynamic. An important factor that may affect the rate of predation on artificial nests is the abundance of natural prey (mainly rodents), which can vary significantly between years. According to the alternative prey hypothesis, rodent-eating predators (which predominate the predator communities of temperate Europe) may periodically, during times of low availability of their main prey, suppress the numbers of alternative prey (Dunn 1977, Angelstam *et al.* 1984, Norrdahl & Korpimäki 2000). Chicken eggs in artificial nests may be considered such alternative prey; thus, during years of low rodent densities, the rates of predation on artificial nests can increase.

Long-term increase in predation rates

The high variability in predation rates observed in many studies presents problems, mainly because the predation rate recorded during any one trial (replicate) may not reflect the overall rate of predation. Furthermore, as the number of repeated trials increases, the potential for predator learning probably also increases. Some studies failed to find any changes in predation rates between consecutive trials (Wilson *et al.* 1998, Matessi & Bogliani 1999), while others did, and they showed that the proportion of depredated nests increases with the duration of their exposure (Martin 1987, Esler & Grand 1993, Whelan *et al.* 1994, Huhta *et al.* 1996, Ackerman *et al.* 2004). In each year of the present study, predation rates increased during the nine-day experimental session (M. Brzeziński unpubl. data), which could be explained by short-term predator learning. Furthermore, despite some year-to-year variation, a steady increase was seen in overall predation rates in all habitats during the 12 years of study, but it is difficult to speculate on how much long-term predator learning contributed to this trend. In short-lived animals, it is highly probable, due to high population turnover, that nests were predated mainly by new predator individuals each year with no previous experience of encountering chicken eggs in the experimental transects. In addition, these “egg resources” were available temporarily (9

days per trial), not aggregated (adjacent nests about 100 m apart) and consecutive trials were set up very rarely (once per year): features that would not be expected to facilitate long-term learning. On the other hand, long-term predator learning cannot be excluded in the case of badgers, for example, which may occupy their sets and territories for many years (Kowalczyk *et al.* 2000). Several authors have suggested that corvids may learn to search for artificial nests (Picozzi 1975, Yahner & Wright 1985, Buler & Hamilton 2000), but these birds depredated few nests in the present study. Finally, it should be mentioned that the bias resulting from predator short-term learning, if present, would occur in all habitats and years.

It may also be assumed that year-to-year variation in the predation rate and structure reflects changes in the predators’ community and numbers. Šálek *et al.* (2004) suggested that year-to-year variations in the numbers of mammalian predators might be the reason for different rates of predation observed on artificial nests in subsequent years of an experiment. In general, the abundance of most predators that contributed to predation of artificial nests recorded in the present study has increased in Poland in recent years. Hunting bags of two invasive predators, the American mink and racoon dog, as well as native carnivores (red fox, badger and polecat), have increased in Poland, which most probably reflects their increasing abundance (Budna *et al.* 2006). The abundances of the raven and jay have also increased over the last few years (Chylarecki & Jawińska 2007). However, interpretation of observed trends in survival rates as an increase of predator numbers should be done with caution because we do not have adequate information on predator community dynamics in the study area. The rapid increase in egg-robbing activity by badgers during the final years of this study undoubtedly resulted from an increase of the local population and the establishment of new badger sets and territories overlapping the experimental transects. Badgers appeared in the area in 2004 (they inhabited old badger sets, which for unknown reasons were abandoned many years before) and in the following years their nest predation increased in all habitats. Hounscome and Delahay (2005) concluded that

any increase in badger abundance increases the predation pressure on birds.

An important unanswered question is, to what extent did the observed increase in predation pressure on artificial nests reflect the long-term survival rates of real bird nests? Our results suggest that some trends in predation pressure on real nests may exist, but this topic requires further study.

Methodological implications

The extensive literature on experiments conducted using artificial nests mainly describes the results of short-term studies. For instance, in the first 20 papers from the ISI database describing experiments with artificial nests, the mean duration of the studies was 1.85 years, with 55% reporting studies of only 1 year (keywords: “artificial nests”, sorted by relevance). Our results indicate that short-term studies of nest predation are prone to year-to-year variation in patterns of predation. Consequently, contribution of particular species to the overall level of predation may easily be over- or underestimated if studied during periods as short as one or two years. Short-term studies, combined with other reported drawbacks of employing artificial nests for investigating predation on real nests, makes the use of this method even more questionable.

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